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A Review of the Genera Grouse (Aves, Tetraoninae)

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INTRODUCTION

The grouse comprise a Holarctic group of gallinaceous birds of considerable economic importance, currently arranged (Peters, 1934) in 11 genera and about 18 species (there may be as few as 14 species). More than half of the genera accepted by Peters are monotypic, and congeneric sympatric species are found only within the genera *Tetrao* and *Lagopus*. To enable a better appraisal of tetraonine relationships, I undertook the study of several facets of grouse morphology and biology, the results of which are presented herein. I realize that behavioral, biochemical, and further anatomical information is required before a definitive taxonomy of groups such as the Tetraoninae is possible. However, while we await such information, full taxonomic use should be made of external morphological characters. That this has not previously been accomplished for the Tetraoninae is suggested by some of my results.

SOME MORPHOLOGICAL FEATURES OF GROUSE EGG COLOR

Egg color is, of course, subject to the effects of natural selection; hence convergence in color and markings may be expected to occur. Although

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evaluation of convergence is difficult, similarities in egg color among grouse may provide corroborative evidence for relationship, when considered with other characters. Grouse have eggs similar in color to those of certain other phasianid species, but variation within the subfamily is of some taxonomic significance.

Egg color is summarized for the various genera of grouse as follows:

Tetrao: Eggs very large, pale, buffy with a yellow cast, and sparsely spotted with fine dots, or occasionally with heavier spots or blotches.

Lyrurus: Eggs large, colored like those of *Tetrao*, but more blotched.

Lagopus (*lagopus*, *mutus*, "scoticus"): Eggs medium-sized, white to red-brown, heavily or even entirely blotched and spotted with black and brown.

Lagopus leucurus: Eggs medium-sized, white to pale, reddish buff, with scattered small to medium blotches and fine spots.

Canachites, *Falcipennis*: Eggs pale buffy to reddish, and occasionally white; otherwise like those of *Lagopus leucurus*.

Dendragapus: Eggs like those of *Lagopus leucurus*, *Canachites*, and *Falcipennis*, though larger, and with the background color tending more toward white.

Centrocercus: Eggs pale buffy, with grayish to bluish cast, marked with spots; blotches absent, or scattered and small if present; eggs very large.

Tetrastes: Eggs small, pale white to reddish, with scattered spots, and (in some) scattered small brown blotches. Markings usually very sparse in *T. bonasia*, but larger and more extensive in *T. sewerzowi*. More strongly marked eggs of *Tetrastes*, especially those of *T. sewerzowi* (Beick, 1927) are like those of *Canachites*, but smaller.

Bonasa: Eggs small, white to cream-colored (occasionally buff), unmarked or very faintly, sparsely, and finely spotted with brown or reddish. Like the less spotted eggs of *Tetrastes*.

Tympanuchus: Eggs olive to white, with very faint (or no) fine brown spots.

Pedioecetes: Eggs olive to olive-brown, unmarked, or with a few scattered fine brown spots.

Thus, the eggs of *Tympanuchus* and *Pedioecetes* are distinctive in their olive tone, and those of *Bonasa* are distinctive in being generally unmarked. Typical *Centrocercus* eggs are distinctive as well, but those with little blue-gray cast are very like the eggs of *Tetrao*. The very heavy markings of most species of *Lagopus* render their eggs distinctive, but *Lagopus leucurus* has eggs identical with those of some *Canachites*. Eggs of *Lagopus leucurus*, *Canachites*, *Falcipennis*, *Dendragapus*, *Lyrurus*, *Tetrao*, the more marked eggs of *Tetrastes*, and the paler eggs of *Centrocercus* are very similar. Except for the obvious egg-size differences, there exist among *Lagopus leucurus*, *Canachites*, *Falcipennis*, *Dendragapus*, *Lyrurus*, and *Tetrao* only average differences in the tone of the background color and the extent of markings.

A few similarities between grouse and other phasianids should be noted. The *Odontophorinae* (New World quail) generally have un-

marked white eggs, but the few having markings, namely, *Lophortyx* and *Callipepla* (marks faint), resemble those of *Canachites*, *Lagopus leucurus*, and *Tetrao*. Turkeys have eggs similar in color to those of grouse, the eggs of *Meleagris* being very like those of *Tetrao*, and the more blotched eggs of *Agriocharis* resemble those of *Lyrurus*. The olive color shown by some eggs of *Phasianus* (sp.) is very like that of *Tympanuchus* and *Pediocetes*. Among other phasianine genera, *Tetraogallus* and *Lophophorus* have eggs very like those of *Tetrao*, and *Coturnix* eggs resemble the eggs of ptarmigans.

NATAL PLUMAGES

Color patterns of downy young grouse vary within the range of patterns observed elsewhere in the Phasianidae, as, for example, in *Perdix perdix* and *Colinus virginianus* (representing the subfamilies Phasianinae and Odontophorinae, respectively). The major pattern in the Tetraoninae features a variegated brown and light-colored back, with the brown continuing forward onto the crown, various facial marks, and clear yellowish or grayish white under parts.

A black-bordered, rufous brown crown patch is present in *Canachites*, *Falcipennis*, *Lagopus* (border poorly defined in *L.* "scoticus"), and *Lyrurus*. The black border is lacking in *Bonasa* and generally lacking in *Tetrastes*, although these genera do exhibit a rufous crown that forms a patch in *T. sewerzowi*, but not in *T. bonasia* and *Bonasa*. Some traces suggestive of the crown patch are evident in *Dendragapus*, *Tetrao*, and *Centrocercus*. *Pediocetes* and *Tympanuchus* are the only forms lacking any indication of the brown crown patch.

Unlike the back markings (see below), the head markings are easily discernible, and they are diagnostic. One such mark found throughout the subfamily, as well as in certain phasianids (e.g., *Perdix*), is a short, dark streak on each side of the mandible near its base. These streaks vary in size, even within species; they are often so small as to pass undetected on cursory examination, and occasionally they are altogether lacking. Most grouse also exhibit a large or small loral mark, which connects posteriorly with a dark supraorbital line and, in certain grouse (*Lagopus* sp.), a dark malar line. The loral mark extends toward the eye and is continuous with the postocular line to form an eye stripe in other grouse (*Tetrao*, *Lyrurus*, *Centrocercus*, *Tetrastes*, and some specimens of various species of *Lagopus*, and observed as a tendency in some specimens of *Canachites*). The loral spot is indistinct or obsolete in *Bonasa umbellus*, and entirely lacking in the prairie grouse (*Tympanuchus*, *Pediocetes*).

The frontal mark of grouse appears to be a remnant of the black margin around the former anterior end of the brown crown patch. Reduction of the anterior part of the black-bordered crown patch, with loss of the brown color and restriction of the black border, would produce the typical frontal mark. This mark occasionally connects with the dark streaks alongside the mandible. A frontal mark is present in *Pediocetes*, *Tympanuchus*, *Lyrurus*, *Tetrastes*, *Centrocercus*, *Dendragapus*, and some specimens of *Bonasa* (vague), *Lagopus*, and *Canachites*. The mark is further restricted, splitting into two or even three small spots in *Tetrao* (some specimens), *Lagopus leucurus*, *Dendragapus*, and *Centrocercus*.

Other marks on the crowns of some grouse have apparently also been derived from the black margin of a brown crown patch that was probably present in ancestral forms. Thus, the central crown spot, two lateral ones, and a posterior black line leading to the back in *Tympanuchus* appear to be remnants of a black-bordered, brown crown patch that is lacking in these grouse. A similar derivation appears likely for the central crown spot and two lateral crown spots (more anterior, nearer the orbit than in *Tympanuchus*) of *Pediocetes*, and also for the vaguely connected "necklace" of three marks on the hind neck in that genus. *Dendragapus* exhibits a central crown mark which connects with the frontal spot, two lateral stripes (in some cases obscure), and, posteriorly, a poorly defined brown area bordered by almost obsolete darker marks. *Centrocercus* has a very broken pattern of marks on the crown and hind neck; significantly, some specimens show faint indications of a central occipital brown area bordered by black. Two specimens of *Tetrao parvirostris* have a frontal mark similar in configuration to that of *T. urogallus*, but, unlike the latter, they exhibit an arrangement of dark crown marks around a slightly rufous area, suggesting occurrence of a dark-bordered, chestnut or rufous crown patch in the ancestors of *Tetrao*. Hence, although the discrete brown crown patch of other grouse is not discernible as such in *Dendragapus*, *Tetrao*, *Centrocercus*, *Tympanuchus*, and *Pediocetes*, their patterns suggest derivation from ancestral grouse the downy young of which possessed such a patch.

A dark "eyebrow" mark is present in the *franklinii* group of *Canachites canadensis*, *Falcipennis*, some specimens of *Lagopus lagopus* and *L. mutus*, *L. leucurus*, *Tetrao*, *Centrocercus*, *Dendragapus* (traces only), and *Bonasa*. It is also present and continuous with the loral mark in *Tetrastes*, and is vaguely suggested in *Lyrurus*. *Pediocetes* and *Tympanuchus* lack any indication of this mark. Other head markings of some grouse are: one small, and (usually) two larger, occasionally fused, postocular spots in *Pediocetes* and *Tympanuchus*; a postocular stripe in all grouse; a rictal mark

and distinct or vague malar line in *Lyrurus* and *Tetrastes*; and nostril and malar spots in *Centrocercus*.

The tarsi of all grouse are feathered in the natal as well as succeeding plumages. The feathering is most extensive in the genus *Lagopus*, in which it extends nearly to the ends of the toes. *Lagopus leucurus* and *L. "scoticus"* have less feathering of the toes than other ptarmigans. In *Bonasa* and *Tetrastes* feathering is restricted to the upper half of the tarsi. Additionally, the tarsal feathers in these two genera often occur only on the anterior tarsal surface, and they are sufficiently short as to allow the entire tarsus to be seen from a lateral view.

The general tone of the dorsum is yellow or buff and brown in *Canachites*, *Falcipennis*, *Tetrao*, *Lyrurus*, *Bonasa*, *Tetrastes*, *Tympanuchus*, *Pediocetes*, most species of *Lagopus*, and some races of *Dendragapus obscurus*, whereas it is dark brown and gray in *Lagopus leucurus*, some races of *Dendragapus obscurus*, and *Centrocercus*. Markings on the back are difficult to analyze, partly because of the great variability in pattern, but chiefly because poor preparation of specimens and early growth of juvenal interscapular feathers obscure much of the back region in most available specimens of downy young grouse.

The under parts of downy young grouse are colored as follows: yellow in *Canachites*, *Falcipennis*, *Lagopus lagopus*, *L. mutus*, *Lyrurus*, *Tetrao*, *Pediocetes*, and *Tympanuchus*; pale yellowish white to white in *Bonasa*, *Tetrastes*, and some races of *Dendragapus obscurus*; and grayish white in *Lagopus leucurus*, some races of *Dendragapus obscurus* (see colored plate in Moffitt, 1938), and most individuals of *Centrocercus* (occasionally yellowish white). The only markings found on the under parts of grouse chicks are occasional traces of barring on the sides and flanks (in some individuals of *Dendragapus* especially), and a distinctive, brown-bordered, buff band across the lower throat in *Centrocercus*.

Another important marking in downy young grouse is a brown "heel" spot, found on feathers just above and on the inside of the posterior joint between the tarsometatarsus and tibiotarsus. This spot, either isolated or connected with a brown thigh patch, is found in all grouse except *Tetrastes*, *Bonasa*, *Tetrao*, *Pediocetes*, and *Tympanuchus*.

On the basis of natal plumage characteristics, *Tympanuchus-Pediocetes* forms a distinctive group of grouse, and *Bonasa-Tetrastes* is a moderately distinctive group. The remaining genera form a gradient series of stages. Within this continuum *Lagopus lagopus*, *L. "scoticus,"* *L. mutus*, *Canachites*, and *Falcipennis* are very similar, whereas the *Tetrao-Lyrurus* group is separable from these in one direction, and in another direction *Lagopus leucurus* and *Dendragapus* tend toward the extreme represented by *Centrocercus*.



I. ABNORMAL CANACHITES



6. ABNORMAL DENDRAGAPUS



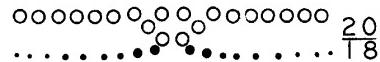
2. LAGOPUS



7. DENDRAGAPUS



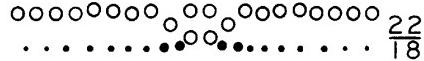
3. ABNORMAL LAGOPUS



8. DENDRAGAPUS



4. TYMPANUCHUS



9. ABNORMAL DENDRAGAPUS



5. ABNORMAL TYMPANUCHUS



10. CENTROCERCUS

FIG. 1. Pattern of rectrices and greater upper tail coverts in some grouse. The feathers are shown diagrammatically as if a section were made through the feathers just above the skin. Rectrices are shown by circles; greater upper tail coverts, by dots. The number of rectrices is indicated over the number of greater covers at the right of each figure. Normal patterns (2, 4, 7, 8, 10) represent the average condition found in species of the genus indicated; the abnormal patterns are discussed in the text. The feathers are shown in relation to one another within each pattern, but the various patterns are not drawn to scale. Directions are as if the birds were facing down the page, i.e., down is anterior, up is posterior, right is to the left of the bird, and left is to the right of the bird.

NUMBER OF RECTRICES

A character to which major importance has been attached (e.g., Elliot, 1864; Ridgway and Friedmann, 1946) in delimiting the genera of grouse is the number of rectrices. A study of tetraonine genera disclosed that this feature is more variable than has been supposed. I investigated the pattern and number of rectrices in North American, and to a lesser extent Eurasian, species of grouse, using specimens in the United States National Museum (which has specimens of all species of grouse). The use of alcohol to moisten feathers of study skins for better examination of the bases of feathers was shown to me by Mrs. Vesta Stresemann. For the purposes of this investigation, I moistened the upper tail coverts with a cotton wad dipped in isopropyl alcohol. The moistened feathers are then easily pushed aside, facilitating an examination of the bases of the rectrices and upper tail coverts. The alcohol evaporates during the course of the examination; then the feathers are easily put back in their normal positions.

The rectrices of grouse are very closely associated with their greater upper tail coverts. The central rectrices are usually anterior (dorsal) to the main line of rectrices (fig. 1). The central greater upper tail coverts are more closely applied to the bases of the central rectrices than are the other coverts to the remainder of the rectrices. Indeed, both the line of rectrices and the line of greater upper tail coverts often appear to radiate outward from the central rectrices (fig. 1). This arrangement, and the similarity of the first (and occasionally the second) rectrices to the greater upper tail coverts in many grouse, suggest a close developmental relationship between these coverts and the rectrices. An increase in rectrix number is accompanied by a corresponding increase in the number of greater upper tail coverts. It is possible that additional rectrices represent modified greater upper tail coverts that move into the line of rectrices, but in at least some instances (see discussion of *Tympanuchus* below) rectrices are added at the outer ends of the line of rectrices, rather than centrally.

The number of rectrices in the genus *Dendragapus* is usually noted as 20 (Ridgway and Friedmann, 1946, p. 67). An examination of three specimens of *Dendragapus obscurus obscurus* disclosed that all had but 18 rectrices. Such a result led to study of 168 specimens of seven subspecies of *D. obscurus*. The results are presented in tables 1 and 2. It is apparent from these data that: (1) *Dendragapus obscurus* has a highly variable number of rectrices; (2) despite this variation, subspecies of this grouse tend to have either 18 rectrices or 20 rectrices; and (3) the *fuliginosus* subspecies group tends to have 18 rectrices and the *obscurus* group 20 rec-

TABLE 1
NUMBER OF RECTRICES IN *Dendragapus obscurus*^a

Form	Number of Rectrices							<i>N</i>
	16	17	18	19	20	21	22	
<i>obscurus</i> group								
<i>obscurus</i>	1	0	32	4	6	—	—	43
<i>richardsonii</i>	—	—	5	2	19	0	1	27
<i>pallidus</i>	—	1	1	2	22	0	1	27
<i>oreinus</i>	—	—	2	0	7	—	—	9
<i>fuliginosus</i> group								
<i>fuliginosus</i>	—	—	16	1	2	—	—	19
<i>sitkensis</i>	—	—	14	1	2	—	—	17
<i>sierrae</i>	3	1	21	1	—	—	—	26
Total	4	2	91	11	58	0	2	168

^a One hundred sixty-eight specimens in the collection of the United States National Museum.

trices, except for *D. o. obscurus*, which resembles the *fuliginosus* group in having only 18 rectrices. There was no marked difference between the sexes, although within each subspecies the birds with fewer than normal rectrices tend to be females, and those with more than the normal number of rectrices tend to be males. Specimens with an odd number of rectrices represent true asymmetry, for they show no sign of a missing rectrix.

The patterns of rectrices and greater upper tail coverts of specimens of *Dendragapus obscurus* with a subnormal, normal, and supernormal number of rectrices are shown in figure 1. There is evidence of crowding around the central rectrices as the number of rectrices increases. The line of rectrices becomes uneven at about rectrices 7. The second rectrices come to occupy positions more directly behind (below), and less lateral to the central pair. The third rectrices more closely adjoin the first, so that the second pair is concealed when one views the tail from

TABLE 2
NUMBER OF RECTRICES IN THREE SPECIES OF GROUSE

Species	Number of Rectrices									<i>N</i>
	14	15	16	17	18	19	20	21	22	
<i>Canachites canadensis</i>	2	1	60	2	1	0	0	0	0	66
<i>Dendragapus obscurus</i>	0	0	4	2	91	11	58	0	2	168
<i>Bonasa umbellus</i>	1	0	6	0	380	5	4	0	0	396

above. The line of greater upper tail coverts remains even, as the number of rectrices and greater upper tail coverts increases. There is usually one fewer pair of coverts than rectrices.

An examination of 66 specimens of *Canachites canadensis* (including 25 of *C. c. franklinii*) disclosed that all but six have the normal 16 rectrices. The normal pattern is similar to that of normal *Lagopus* (fig. 1). The six aberrant spruce grouse have 14, 15, 17, or 18 rectrices, as indicated in table 2. In all but one of these aberrant birds the number of greater upper tail coverts is two (even number of rectrices) and one (odd number of rectrices) fewer than the number of rectrices. The one exception has 14 rectrices and 14 coverts. The pattern of the rectrices in the three specimens with a supernormal number of rectrices is uncomplicated, with no crowding about the central pair, and no distortion of the even line of rectrices. Seven specimens of *Falcipennis falcipennis* have 16 rectrices and 14 or 16 greater upper tail coverts arranged like those of *Canachites* and *Lagopus*.

Five specimens of each of the three species of *Lagopus* were examined. Except for one bird, these have 16 rectrices and 14 or 12 greater upper tail coverts. The central greater upper tail coverts are large and closely applied to the lateral bases of the central rectrices (fig. 1). The second rectrices are usually visible from above, but in several instances they are positioned rather behind the first pair, and thus are hidden from view. A single specimen of *Lagopus leucurus peninsularis* (U.S.N.M. No. 241267) has 18 rectrices arranged in an otherwise normal manner, and 14 greater upper tail coverts (fig. 1). Additional specimens of this race were then examined and were found to have the normal number of rectrices.

The tails of several specimens of *Tetrao urogallus*, *T. parvirostris*, and *Lyrurus tetrix*, and one specimen of *L. mlokosiewiczi* were examined and were found to have 18 rectrices and 16 or 14 greater upper tail coverts. The arrangement of the rectrices is uncomplicated, with the row of rectrices extending laterally from between rectrices 1 and 2. The second rectrices are usually directly behind (or below) the first pair, and they are more or less hidden from view.

Centrocercus urophasianus regularly has 18 or 20 rectrices, and the number of greater upper tail coverts is usually equal to the number of rectrices (fig. 1). The line of rectrices extends laterally from the second pair, or from between the first and second pair.

Rectrices were counted in 20 specimens (representing three subspecies) of *Tympanuchus cupido*, 10 specimens of *T. pallidicinctus*, and 25 specimens (representing four subspecies) of *Pedioecetes phasianellus*. The tail coverts and rectrices of five specimens of *T. cupido*, three of *T. pallidicinctus*, and

five of *P. phasianellus* were studied in detail. All these specimens have 18 rectrices. Two specimens of *T. cupido* show 14 greater upper tail coverts, whereas the other specimens of that species and of *T. pallidicinctus* and *P. phasianellus* that were studied have 16 greater upper tail coverts. In these grouse the second rectrices are almost lateral to the central rectrices, rather than behind (or below) them. Hence the rectrices form almost a straight line. The central greater upper tail coverts are situated somewhat more laterally to the central rectrices than they are in most other grouse. No differences in arrangement were evident among these three species. The specimens of *Tympanuchus cupido* that were examined included one specimen of *T. c. attwateri* (U.S.N.M. No. 357264) with an asymmetrical tail pattern. This bird has 18 rectrices, but 10 are on the right side and eight are on the left (fig. 1). There is no evidence of a missing rectrix on the left side. The greater upper tail coverts are symmetrical, numbering 14, but the greater under tail coverts are also asymmetrical, with 10 on the right and nine on the left. The additional rectrix on the right side is a very small (63 mm.) rectrix 10. The ninth rectrix on the right side is normal (75 mm.) in length for an outer rectrix of *T. cupido*. The outer (eighth) rectrix on the left side measures 81 mm. in length and is identical to right rectrix 8. Thus, the gain and loss of rectrices involve the outermost feathers; the additional right rectrix is rectrix 10, and the rectrix lacking on the left is rectrix 9. The addition and loss of rectrices in this individual suggest that a very large sample of prairie grouse would contain a few birds with 16, 17, 19, or 20 rectrices.

The ruffed grouse (*Bonasa umbellus*) usually has 18 rectrices. An examination of 396 specimens of 10 subspecies of ruffed grouse gave the results shown in table 2. The distribution of the rectrices is similar to that figured (fig. 1) for *Tympanuchus*, except that the second rectrices are situated more posteriorly (or ventrally) with respect to the central rectrices, and the number of greater upper tail coverts is frequently 14 instead of 16. The nine specimens with more rectrices than normal show effects of crowding in that the rectrix line is somewhat uneven, and there is a greater tendency for the second rectrices to be directly behind the central rectrices. The reduction in number of rectrices results in patterns approaching those shown (fig. 1) for *Lagopus*. Five specimens of *Tetrastes bonasia* had 16 rectrices and 14 greater upper tail coverts, arranged like those of *Lagopus* (fig. 1). Available specimens of *T. sewerzowi* were molting rectrices and tail coverts, but the number of rectrices is 16, and there appear to be 14 greater upper tail coverts arranged as in *T. bonasia*. It seems probable that a sufficiently large series of *Tetrastes bonasia* and *T.*

TABLE 3
NUMBER OF RECTRICES IN GENERA OF GROUSE

Genus	Usual Number of Rectrices	Range of Variation
<i>Tetrao</i>	18	?
<i>Lyrurus</i>	18	?
<i>Lagopus</i>	16	14-18
<i>Dendragapus</i>	18-20	16-22
<i>Canachites</i>	16	14-18
<i>Falcipennis</i>	16	?
<i>Centrocercus</i>	18-20	?
<i>Bonasa</i>	18	14-20
<i>Tetraastes</i>	16	?
<i>Tympanuchus</i>	18	? (probably 16-20)
<i>Pediocetes</i>	18	?

sewerzowi would turn up a few birds with 18 rectrices, but the probability remains to be demonstrated.

Little attention was devoted to the under tail coverts because of the difficulty of examining that area in museum skins (the legs of the specimens are in the way). Also, the greater under tail coverts are obscured by the closely associated lesser coverts, to a greater degree than the greater upper tail coverts. However, the under tail coverts were examined in a few cases. It is evident that the greater under tail coverts more often correspond in number to the number of rectrices than do the greater upper tail coverts. The greater under tail coverts appear to exhibit asymmetry when the rectrices are asymmetrical in number; no such asymmetry was noted in the greater upper tail coverts.

The variation in number of rectrices among the genera of grouse is summarized in table 3. This variation mitigates against the utilization of the number of rectrices as a major taxonomic character for tetraonine genera.

ANALYSIS OF GENERA

The following analysis of the genera of grouse is based on a review of their characters as stated in the literature, the results of the above morphological investigations, and biological considerations consistent with a modern generic concept. Before evaluating the genera of grouse, I briefly discuss the generic concept that I espouse.

The genus and other higher taxonomic categories are, in contrast to the species, arbitrary. The functions of the higher categories are utili-

tarian. The proper use of these categories depends on a maintenance of their positions in the hierarchy, i.e., the various levels must not impinge upon one another. Thus, the genus must not approach either the next higher (family) or next lower (species) level, if it is to prove useful.

A genus is essentially a group of species that are usually related more closely to one another than any one of them is to any species of another genus. Ornithology is (not alone) plagued with polytypic species and superspecies which have been considered valid "genera" (examples are given below; see also Amadon's [1943] discussion of *Sturnus vulgaris*), thus distorting the classification of the groups involved. A superspecies should be considered as a single "species" for the purpose of evaluating the composition of genera, for, if its component species are considered separately, it becomes difficult or impossible to include other species in the genus, i.e., the superspecies becomes a "genus."

Amadon (1943, p. 1) long ago pointed out that the "modern broadening of the species concept must be accompanied by a compensatory adjustment in the genus concept if the genus is to retain its importance." The widespread acceptance of the biological species concept (Mayr, 1963) should certainly aid us in properly separating the level of the genus from that of the species. If the genus can be divested of its encumbrance of species-affiliated characters, such a separation of these categories can be achieved. Sibley (1957) noted the dangers inherent in taxonomic utilization at the generic level of characters fundamentally involved in isolating mechanisms at the species level. The completion of the process of speciation is marked by the ability of the newly evolved species to exist in sympatry without interbreeding. The existence of sympatric congeneric species provides the only certain means of eliminating as generic characters those often blatantly obvious features of closely related forms that are involved in their interactions on the species level. For this reason I believe that at least one instance of sympatry should occur among the species of most (but not all) genera.

Since a genus is a group of related species, it follows that monotypic genera are to be avoided unless they are so distinctive that their inclusion in another genus would seriously distort that genus. I agree with Mayr, Linsley, and Usinger (1953, pp. 48-49) that monotypic genera should be discouraged by requiring their recognition only if the morphological gap separating them from other genera is considerably greater than those gaps existing between "normal" genera.

TETRAO LINNAEUS, 1758, AND LYRURUS SWAINSON, 1831

The capercaillies (*Tetrao urogallus* and *T. parvirostris*) and black grouse

(*Lyrurus tetrix* and *L. mlokosiewiczi*) are large grouse inhabiting coniferous forests and coniferous forest-edge situations in the Palearctic. The two genera are closely related, and they have sometimes been considered congeneric (Voous, 1960). Morphological features that have been used to separate *Tetrao* and *Lyrurus* are related to their displays, and might be expected to differ in sympatric, closely related species, such as the capercaillies and black grouse. These characters include: the peculiarly shaped tail of *Lyrurus* versus the "normal" tail of *Tetrao*, the partly metallic plumage of males of *Tetrao* compared with males of *Lyrurus*, and the elongate neck feathers of male capercaillies compared with black-cocks. I do not feel that these differences are taxonomically utilizable at the generic level (see further discussion of these species below) and consider them congeneric.

As do the ptarmigans, species of *Tetrao* have relatively short toes and long tarsi. Capercaillies and black grouse have unfeathered toes, although the intertoe membranes may be heavily feathered. Their tails are long, variable in form and usually graduated, and there are normally 18 rectrices. They never have a predominantly white plumage, although males of *T. tetrix* and *T. mlokosiewiczi* show a considerable amount of white. The capercaillies and black grouse are sexually dimorphic in plumage and size, and are polygamous, exhibiting highly ritualized "lek" behavior. Males have inflatable red superciliary "combs," and either modified erectile neck feathers or outwardly curved outer rectrices. Males are mostly black or blackish in color, and may exhibit a metallic sheen, whereas females are brownish, much like female ptarmigans (especially *T. tetrix* and *T. mlokosiewiczi*). The natal plumage of *Tetrao* is yellowish in general tone. There is a black-bordered brown crown patch, or brown marks suggestive of one. A loral mark is present, and it continues to the eye and posterior to the eye as a postocular line. A frontal mark (or marks) and a superciliary mark are also present. The eggs of *Tetrao* are large and pale buff to yellowish, sparsely to moderately spotted or blotched with brown (the eggs of *T. mlokosiewiczi* figured by Oates, 1901, pl. 2, bridge the gap between the finely spotted eggs of capercaillies and the more marked eggs of *T. tetrix*).

This combination of characters strongly distinguishes *Tetrao* from other grouse, except perhaps *Lagopus*. However, *Tetrao* is generically separable from *Lagopus* on the basis of the lack of feathering on the toes, the absence of white plumages and less complex sequence of plumages and molts, and the complex social behavior and display-associated morphological specializations of the males. Similarities between *Lagopus* and *Tetrao* include: the tendency toward white plumage in *Tetrao*; the relative

size of the toes and tarsus; the plumage resemblance of females of *Tetrao* and *Lagopus*; the ecological replacement of ptarmigans by black grouse and capercaillies at the edge of the tundra (Voous, 1960); and resemblances in natal plumages of the two genera. There are also a considerable number of natural hybrids (Gray, 1958) between several species of *Tetrao* (*urogallus*, *tetrix*) and both Palearctic ptarmigans (*L. lagopus*, *L. mutus*). From this evidence it appears that *Tetrao* is closely related to *Lagopus*. Furthermore, the plumage patterns of *Tetrao* (especially *T. mlokosiewiczi*, *T. tetrix*, and *T. parvirostris*) seem readily derivable from an essentially ptarmigan-like plumage. The complex behavior and associated morphological features, and the number of rectrices in *Tetrao*, suggest that the direction of evolution has been from a generalized ancestral grouse toward the more specialized black grouse and capercaillies. It is hence suggested that the ancestor of *Tetrao* was a ptarmigan-like predecessor of modern species of *Lagopus*. Certainly *Tetrao* bears no close resemblance to existing species of other grouse genera (*Falcipennis*, *Tetrastes*) occurring in the Palearctic. The ptarmigans, black grouse, and capercaillies thus appear to constitute a major monophyletic line of grouse.

The species of *Tetrao* comprise two superspecies, previously designated as genera (*Tetrao*, *Lyrurus*). Within these superspecies it is not completely clear whether the separate entities constitute biological species. *Tetrao* ("Lyrurus") *tetrix* and *T. mlokosiewiczi* are allopatric (there is a gap of approximately 550 miles between their ranges in central Russia and the Caucasus, respectively), very closely related forms. I judge that *mlokosiewiczi* is more like the ancestor of the two forms than is *tetrix*. Differences between the two forms include a less specialized tail in *mlokosiewiczi*, the lack of a white wing bar in that form, and plumage differences between females of the two. Further study of *T. mlokosiewiczi* may demonstrate that these differences are not sufficient to warrant specific status of this form, but I prefer to retain them as separate species at the present time. The two capercaillies, *T. urogallus* and *T. parvirostris*, meet and apparently overlap (Dementiev and Gladkov, 1952) in western Siberia, but they hybridize (in one area 12% of courting male capercaillies were hybrids; Kirpichev, 1958), and the situation regarding the extent of their overlap is unclear. The differences between these species include bill size, minor differences in plumage of the females, and some differences in natal plumage pattern. I prefer to maintain the two forms as separate species (within a superspecies), pending further study of their relationships.

Recognition of separate species of black grouse and capercaillies should not obscure the fundamental and close interrelationship of these two

superspecies. The ecological replacement of the two groups (Voous, 1960), and the high frequency of hybridization and relative fertility of their hybrids (Gray, 1958; Voous, 1960), suggest their very close relationship. Likewise, there are strong similarities in their behavior (Höhn, 1953; Lumsden, 1961). Display differences of males appear to be those one would expect to find in closely related, interacting, frequently hybridizing sympatric species (e.g., compare the lowered head and down-curved tail of a displaying male black grouse with the raised head and cocked tail of a displaying male capercaillie; Peterson *et al.*, 1954, p. 166). It seems likely that the ancestral species of *Tetrao* gave rise to the ancestral species of black grouse, and the ancestral capercaillie. These had barely evolved to the level of species when populations of each became geographically isolated. Despite the existence of morphologically well-differentiated forms of each, the hybridization, behavioral interactions, and competitive interactions between black grouse and capercaillies bear evidence to the fact that they are themselves in the final stage of speciation.

LAGOPUS BRISSON, 1760

The ptarmigans comprise a distinctive group of small to medium-sized grouse which generally inhabit the northern tundra and tundra edge, and alpine situations in more southern mountains. Most of their distinctive features seem adaptively correlated with their far northern distribution, compared with that of other grouse. Their toes are rather short relative to their tarsal length, and their toes as well as their tarsi are feathered. The lateral toe pectinations of other grouse that have unfeathered toes are correspondingly reduced in *Lagopus*. All ptarmigans but two races (*scoticus*, *helveticus*) of *L. lagopus* are largely white in the winter, and all have distinct summer, fall, and winter plumages. Their molts are among the most complicated of bird molts, and, indeed, ptarmigans are in molt most of the time. They are usually monogamous, and the sexes are similar in color. Their tails are rather short and evenly rounded, with unusually long upper tail coverts. The upper tail coverts approach, equal, or even exceed the rectrices in length (the long coverts are white in the winter, when they conceal the usually black tail, and they are brown in the summer, when they conceal the usually white central rectrices). These grouse lack vocal sacs, neck tufts, and the display structures of other grouse, except that males possess well-developed, inflatable, red, superciliary "combs." The usual number of rectrices in ptarmigans is 16, but as few as 14 and as many as 18 have been discovered in some birds. The natal plumage varies from grayish to yellowish in background color; there is a black-bordered, rufous or brown crown

patch, and dark loral, frontal, and various other markings occur. Ptarmigan eggs are white to reddish in color, and they are usually heavily blotched or marked with brown or black.

Their various distinctive features separate the ptarmigans from their relatives, the capercaillies and black grouse (*Tetrao*) and the spruce grouse (*Dendragapus*). *Tetrao* shares certain features with *Lagopus*, and was probably derived from an ancestral ptarmigan-like form (see above). The apparent specializations of *Lagopus* and *Tetrao*, and the lack of extant species intermediate between them and other grouse, render difficult the search for their existing relatives. However, by a process of elimination, *Dendragapus* (including *Canachites* and *Falcipennis*) is the likeliest related genus. There is no evidence for close affinity of *Tetrao* and *Lagopus* with such specialized forms as the sage grouse (*Centrocercus*) and the prairie grouse (*Tympanuchus*). Likewise, *Bonasa* does not appear particularly to resemble *Lagopus* and *Tetrao*, although there are reports of a number of hybrids between species of *Lagopus* and *Bonasa* ("*Tetrastes*") *bonasia* (see citations in Gray, 1958).

Relationship of *Lagopus* with *Dendragapus* is suggested by: the Nearctic center of distribution of *Lagopus* and *Dendragapus*, the relatively simple territorial and courtship behavior of the two genera (Bent, 1932; Yama-shina, 1939; Grange, 1940; Wing, 1946; Peterle, 1955; Lumsden, 1961; Watson and Jenkins, 1964), and the ecological replacement of *Lagopus* by *Dendragapus* (*canadensis*) in the coniferous forest-tundra ecotone. The similar coloration of the eggs of *Lagopus leucurus* and those of several species of *Dendragapus* will be recalled from the above discussion of egg color. A major point is the great similarity of the natal plumage of *Lagopus lagopus*, *L. mutus*, *Dendragapus canadensis*, and *D. falcipennis*. Although this similarity could be due to convergence, such a possibility is mitigated against by the similarity in minor details of pattern. The black tails of most species of *Lagopus* are narrowly tipped with white (in fresh plumage); *Dendragapus falcipennis* has a broadly white-tipped black tail, and the black tail of *D. canadensis franklinii* is often narrowly tipped with white. The displays of male ptarmigans, as well as males of *Dendragapus canadensis* and *D. falcipennis* (citations above), include: a vertical jump or short flight, the cocking and spreading of the tail, the fluffing of neck feathers, and "drumming" or rattling of the wing feathers. A hybrid male *Lagopus lagopus* × *Dendragapus canadensis* was described and figured by Taverner (1932), who mentioned another such hybrid in the same paper. Because of these similarities I feel that *Lagopus* (as well as *Tetrao*) is closely related to *Dendragapus* and probably evolved from a generalized grouse ancestral to modern species of *Dendragapus*.

I recognize three species of *Lagopus*. Considering the magnitude of the morphological differences apparently necessary for sympatric existence among ptarmigans (*Lagopus lagopus* and *L. mutus* throughout the Holarctic region, and *L. mutus* and *L. leucurus* in North America) and other grouse (e.g., *Dendragapus obscurus* and *D. canadensis franklinii*, *Tetrao urogallus* and *T. tetrix*, *Tympanuchus cupido* and *T. phasianellus*), I think that *Lagopus "scoticus"* is conspecific with *L. lagopus*. *Lagopus lagopus* and *L. mutus* exhibit considerable similarity and are closely related, whereas *L. leucurus* is a distinctive species somewhat removed from *mutus* and *lagopus*. Intragenetic hybrids of *Lagopus lagopus* and *L. mutus* are not uncommon (Gray, 1958), but neither has hybridized with *L. leucurus*.

The peculiarities of *L. leucurus* that set it apart from the other ptarmigans are: its very rapid and early postjuvenile molt (its juvenile plumage is reduced, and it essentially progresses from natal plumage to first fall plumage; Short, personal observation), its differently marked and colored eggs (more like those of *Dendragapus* than those of other *Lagopus* species), its distinctive natal plumage, and various features of its adult plumages. These differences from the other ptarmigans probably represent for the most part specializations of the white-tailed ptarmigan, rather than ancestral features that have been lost in *L. lagopus* and *L. mutus*.

DENDRAGAPUS ELLIOT, 1864, *CANACHITES* STEJNEGER, 1885,
AND *FALCIPENNIS* ELLIOT, 1864

Since 1899 *Canachites* has generally been recognized as a genus distinct from *Dendragapus*, although prior to that time it was considered a subgenus of *Dendragapus* (American Ornithologists' Union, 1886, 1895). *Canachites* was separated from *Dendragapus* because of its fewer rectrices, lack of inflatable cervical vocal sacs in males, and certain color differences. The above discussion of the number of rectrices in *Canachites* and *Dendragapus* clearly indicates that this character is not taxonomically useful at the generic level. An examination of museum skins of breeding males of "*Canachites*" *canadensis* disclosed that small cervical vocal sacs are present, as Wing (1946, p. 155) had previously noted. This fact, and the difference in size of the cervical sacs (Ridgway and Friedmann, 1946, pp. 68, 82) in the two subspecies groups (*fuliginosus* and *obscurus* groups) of *D. obscurus*, render the presence or absence of vocal sacs useless as a character separating *Canachites* from *Dendragapus*. The differences in coloration of plumage between *Canachites* and *Dendragapus* appear not to be of taxonomic significance at the generic level.

There exist many similarities between *Canachites canadensis* and *Dendragapus obscurus*, including the following: (1) general body proportions; (2) bill

shape; (3) relative size and shape of the wings; (4) shape of the rather long tail, and its color, which is gray to black, often with a terminal band (white, gray, or chestnut in color); (5) relatively long toes and short tarsi; (6) white mark or line on the sides of the neck; (7) egg color (white to reddish with dark blotches and spots); (8) juvenal plumage (very similar throughout); and (9) drumming flight of males (Wing, 1946, pp. 154–155). A major difference between them not previously noted is their quite dissimilar natal plumages. However, the pattern of *Dendragapus* seems derivable from that of *Canachites* (see above discussion). Also, rather striking differences in natal plumage are found in other congeneric species of grouse, such as *Lagopus leucurus*, *L. lagopus*, and *L. mutus*. I therefore feel that *Dendragapus* and *Canachites* do not warrant recognition as separate (presently monotypic) genera.

The Siberian spruce grouse, *Falcipennis falcipennis*, is obviously closely related to *Dendragapus canadensis*, as clearly noted by Hartlaub in his original description of the species (as *Tetrao falcipennis* Hartlaub, 1855) and by subsequent authors (Dresser, 1903; Taka-Tsukasa, 1935; Yamashina, 1939; Ridgway and Friedmann, 1946). The genus *Falcipennis* was erected by Elliot (1864) solely on the basis of its attenuate outer primaries. Yamashina (1939) compared *F. falcipennis* with “*Canachites*” *canadensis* and *C. franklinii*, and concluded that these three forms comprise a Formenkreis; he merged *Canachites* into *Falcipennis*.

The form of the falcate outer primaries of *F. falcipennis* is shown in figure 2. Although the attenuation of these primaries is remarkable, these feathers are nevertheless quite similar to the fairly narrow primaries of “*Canachites*,” and also to those of *Lagopus* (fig. 2). I agree with Yamashina (1939, p. 9) that the striking over-all morphological similarity of *Canachites* and *Falcipennis* is of greater significance than one morphological modification, the function of which is unknown (do the attenuate primaries produce a special rattling or whistling sound during display, such as that produced by the similarly narrowed primaries of the guan, *Pipile cumanensis*, reported by Chubb, 1916, p. 31?). Elsewhere in the Galliformes, the cracid genera *Chamaepetes*, *Pipile*, and *Aburria*, and a few species of *Penelope* (especially *supericularis* and *granti*), have deeply incised outer primaries. The case of *Penelope* is pertinent, for most species of this genus show no narrowing of the primaries; some species exhibit a slight tendency toward incised primaries; and a few species (noted above) have highly incised outer primaries. Despite this variation, all these species are considered congeneric. Yamashina (1939, p. 9) noted a similar situation in the pigeon genus *Ptilinopus*, in which the occurrence of attenuate primaries was once used for excessive generic and subgeneric splitting,

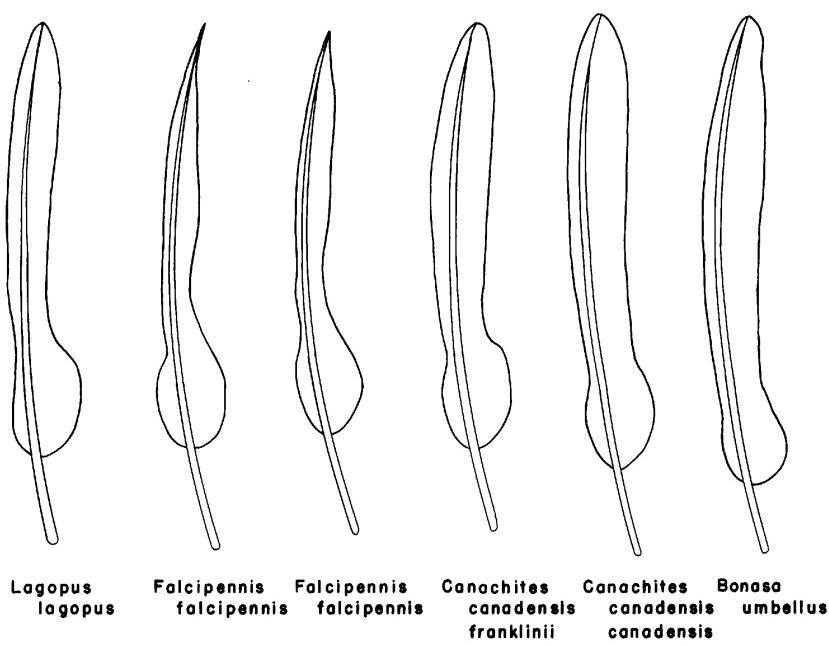


FIG. 2. Shape of the outer primaries of some grouse. The feather drawn is in each case the right eighth primary of a randomly chosen male.

although species with and without modified primaries are now considered congeneric.

In addition to the similarities among these grouse pointed out by Hartlaub (1855) and Yamashina (1939), I note the following: (1) the courtship display of *F. falcipennis* males described by Yamashina and Yamada (1935) and Yamashina (1939) seems almost identical to that of *C. canadensis* described in Bent (1932) and Lumsden (1961); (2) the posterior upper parts of the two species are not so different as Hartlaub and Yamashina have indicated, for some specimens of *C. canadensis* have the transverse back barring reduced to vermiculations very like those of *F. falcipennis*, and occasional individuals of *C. canadensis* exhibit the white shaft streaks typical of *F. falcipennis*; (3) *C. c. franklinii* usually has in fresh plumage a white-tipped tail, very like that of *F. falcipennis*; and (4) the eggs and downy young of *F. falcipennis* figured by Taka-Tsukasa (1939) appear identical with those of *C. canadensis*. Differences between the two species, other than the shape of the primaries, were cited by Hartlaub (1855) and Yamashina (1939). These differences appear at best to separate *canadensis* and *falcipennis* at the species level; in many respects,

the differences are no greater than those found between the conspecific *canadensis* and *franklinii* groups of *C. canadensis*. The differences are not of sufficient magnitude to warrant maintaining *Falcipennis* as a monotypic genus.

Falcipennis and *Dendragapus* were both described on the same page by Elliot (1864, p. 23). I favor the use of *Dendragapus* as the generic name for this group of grouse, as "*Falcipennis*" is obviously a more restrictive appellation (also, *Dendragapus* has line priority over *Falcipennis*). Merging *Falcipennis* and *Canachites* into *Dendragapus* gives proper emphasis to similarities and relationships among these grouse, besides eliminating poorly based monotypic genera. The merger makes sense zoogeographically, suggesting the Nearctic origin of *Dendragapus*, and the close relationship of an isolated East-Siberian species (*falcipennis*) with congeneric North American species.

Among the three species of *Dendragapus*, I consider *D. falcipennis* most like the ancestor of the genus (except for its falcate primaries), and *D. obscurus* the most specialized species. *Dendragapus falcipennis* has the most generalized color pattern, with the least amount of black, vermiculations and white streaks dorsally, and brown-marked central rectrices (in the others, these are similar in color to other rectrices). *Dendragapus canadensis* is barred above, rather than bearing vermiculations (though some do) and white shaft streaks. The natal plumages of *falcipennis* and *canadensis* are very similar to those of the ptarmigans (*Lagopus*). Males of these two species engage in solitary displays and have poorly developed vocal sacs. *Dendragapus obscurus* has the most strongly differentiated natal plumage of this genus. Its rather distinctive adult plumages are mostly gray-black, although there are dorsal vermiculations resembling those of *D. falcipennis*. Its rather well-developed vocal sacs (especially those of the *fuliginosus* group), and tendency toward "lek" behavior (*obscurus* group, Wing, 1946; Hoffmann, 1956), are reasons for considering it somewhat more specialized than *canadensis* and *falcipennis*. Similarities between ptarmigans and the spruce grouse (*D. canadensis* and *D. falcipennis*) are discussed above, and in sections on other genera (see especially the *Bonasa* and *Tetraastes* section). Intraspecific "hybrids" are known both in *D. obscurus* and in *D. canadensis*, and there is one reported interspecific hybrid between these species (Gray, 1958). Several intergeneric hybrids have also been reported (*D. obscurus* × *Tympanuchus phasianellus*; *D. canadensis* × *Lagopus lagopus*; Gray, *loc. cit.*).

I tentatively consider *D. falcipennis* a full species closely related to *D. canadensis*. Detailed studies of *falcipennis* may show that this form is not specifically distinct from *canadensis*. The American spruce grouse (*D.*

canadensis) is polytypic, with one race (*franklinii*) that was once considered a full species. However, the *canadensis* subspecies group interbreeds with *franklinii* in southwestern Alberta and north-central British Columbia (Aldrich in Jewett *et al.*, 1953), and introgression apparently occurs (Short, personal observation). I follow Peters (1934) and the American Ornithologists' Union (1957) in considering conspecific the *fuliginosus* and *obscurus* subspecies groups of *D. obscurus*. These two groups interbreed in a narrow area in Washington and British Columbia (Munro and Cowan, 1947; Jewett *et al.*, 1953), although the frequency of interbreeding has not been established.

CENTROCERCUS SWAINSON, 1831

The sage grouse is the sole species of this relatively distinctive genus. Unique structural modifications associated with territorial and courtship displays are the finely pointed rectrices (numbering 20), the erectile, spiny-shafted feathers of the white neck ruff, and the erectile black neck plumes. Other display structures include cervical vocal sacs which differ morphologically from those of other grouse (Brooks, 1930), and large, erectile, orange-yellow superciliary "combs." In addition to these display structures, the species is unique among the grouse in having a membranous, rather than muscular (gizzard) stomach (Ridgway, 1874); a black belly patch in the juvenal plumage, as well as in all adult plumages; a dark-bordered brown throat patch in the natal plumage; and an elongate, constricted area of the culmen between the nasal fossae. These grouse are strongly sexually dimorphic and polygamous, and they exhibit elaborate "lek" behavior (Patterson, 1952; Scott, 1950). They occupy upland sagebrush plains, a unique grouse habitat. Eggs of the sage grouse are quite like those of *Tetrao*, except that they often show a diagnostic grayish or bluish cast. These characters warrant maintaining *Centrocercus* as a monotypic genus.

The relationships of the sage grouse with other grouse are not clear. It seems unlikely that it is especially close to *Tympanuchus*, although it follows the prairie grouse in most classifications. Its superficial similarity in coloration to the prairie grouse probably reflects convergent evolution in birds occupying somewhat similar (open-country) habitats. I suspect that it evolved from a *Dendragapus*-like ancestor, and that its nearest living relative is *D. obscurus*.

Most suggestive of relationship between *Centrocercus urophasianus* and *Dendragapus obscurus* is the general similarity of their natal plumages. Adult males of *C. urophasianus* exhibit white loral and postocular marks like those of *Dendragapus*, and they have the white throat border char-

acteristic of that genus. Like *D. obscurus*, the sage grouse has orangish superciliary combs. The ventral color pattern of adult male sage grouse consists of a white-bordered dark anterior throat patch, a black posterior throat patch, a white breast patch, and a black lower breast and abdomen. This pattern is easily derivable from that of *D. obscurus*, which has a white-bordered dark anterior throat patch, followed by a dark gray breast and abdomen; the breast feathers are white toward the bases (often showing through), and there often appear white-barred breast feathers. Finally, *D. obscurus* shows indications of "lek" behavior (Wing, 1946; Hoffmann, 1956) from which the more complex behavior of *Centrocercus* (Patterson, 1952; Scott, 1950) could easily have been developed.

TYMPANUCHUS GLOGER, 1842, AND *PEDIOECETES* BAIRD, 1858

Pedioecetes is generally separated from *Tympanuchus* on the basis of its elongate central rectrices, and the lack of the cervical air sacs and elongate neck feathers found in *Tympanuchus* (Ridgway and Friedmann, 1946). However, Shufeldt (1882, p. 658) long ago noted rudimentary cervical "tufts" in some specimens of *Pedioecetes phasianellus*, and this species has functional cervical air sacs (purple in color in *P. p. columbianus*, according to Hart, Lee, and Low, 1950, pp. 18-19) that are conspicuous in some museum specimens. There is very close agreement between these two genera in the characters discussed above. Gray (1958) listed hybrids between *Tympanuchus cupido* and three races of *Pedioecetes phasianellus*. Under certain situations hybridization between them occurs so frequently that the hybrids (which are fertile) may comprise a significant portion of the population (Mayr, 1963, p. 117).

The morphological features of these "genera" do not warrant their separation, even if they were not capable of genetic exchange. Their morphological differences are clearly those that one would expect to find in interacting, closely related species inhabiting open country, where selection due to predation would render species-recognition features less conspicuous than those evolving in woodland forms. The occurrence of natural hybridization between these prairie grouse is proof that they do interact. Hence, I suspect that features such as the elongate tail of *phasianellus* and the neck tufts of *cupido*, as well as differences in their courtship behavior and habitat preference, play a role in limiting their interaction. Since the differences between these "genera" are precisely those that one would expect as a result of competition and selection against hybridization between closely related, congeneric species, such differences are valid for taxonomic use at the species level, but not at the generic level.

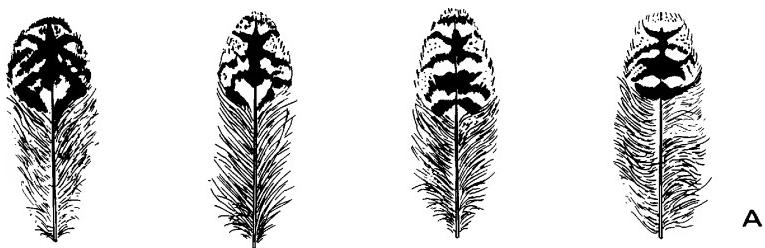
I agree with Shufeldt (1882, p. 700) who, after osteological study of North American grouse, concluded that "little violence would be perpetrated by restricting them [*Pedioecetes*, *Tympanuchus*] to one and the same genus." Indeed, the biological evidence demands merger of *Pedioecetes* with *Tympanuchus*.

Characteristic features of this broadened genus *Tympanuchus* are: the very short, graduated tail (outer rectrices much smaller than central ones, which are elongated in one species); plumage almost entirely barred; sexes very similar; polygamy, with highly developed "lek" behavior; inflatable superciliary "comb"; cervical vocal sacs; under tail coverts longer than short outer rectrices; downy young lacking indications of a crown patch, loral mark, and superciliary mark, and having one central and two lateral crown spots; eggs distinctively olive to olive-brown in tone, and spotless or nearly so; and habitat grassland and grassland-woodland ecotone. These characters are sufficient to separate *Tympanuchus* from other grouse rather sharply. The genus appears to be quite specialized and ancient, for Brodkorb (1964) listed three fossil species going back as far as the Miocene. *Tympanuchus* probably evolved from early pre-*Dendragapus* stock. The only intergeneric hybrid involving *Tympanuchus* is a hybrid of *T. phasianellus* × *Dendragapus obscurus* (Gray, 1958).

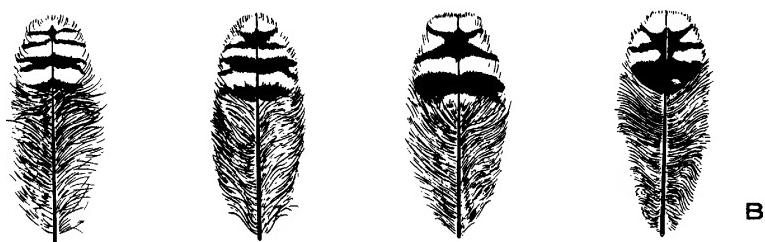
Tympanuchus cupido and *T. phasianellus* are closely related species which are apparently in the final stages of speciation. If so, then what is the status of *T. "pallidicinctus"*? From the interaction and close relationship of *T. cupido* and *T. phasianellus*, it follows that *T. pallidicinctus* should differ from *T. cupido* about as much as does *T. phasianellus*, if *pallidicinctus* has indeed differentiated to the species level. The essential differences between *T. cupido* and *T. pallidicinctus* are (from Ridgway and Friedmann, 1946, pp. 207-220):

CHARACTER	<i>cupido</i>	<i>pallidicinctus</i>
Dark bars of back and rump	Very broad, solid blackish brown (in some cases divided, as in <i>pallidicinctus</i>)	Divided, containing a brown bar enclosed between two narrower black ones
Breast feathers	Brown; tips and subterminal band whitish (actually one to four alternate brown and white bars)	Four to six alternate brown and white bars
Bars on sides and flanks	Brown bars unicolored (actually occasionally bicolored)	Darker bars bicolored, light brown bar enclosed between two dusky ones

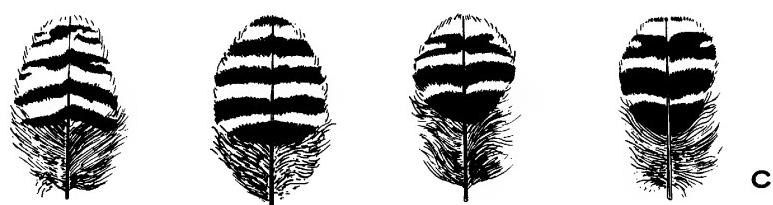
The similarity in barring of the breast and back feathers in *Tympanuchus*



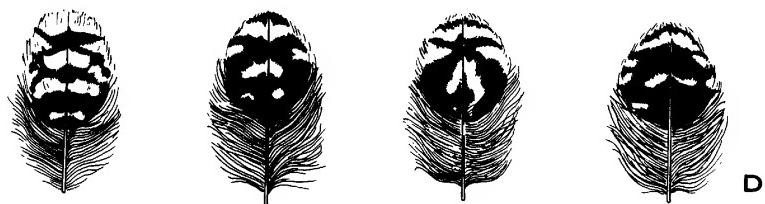
A



B



C



D

FIG. 3. Pattern of breast and back feathers of *Tympanuchus phasianellus* and *T. cupido*. A. Feathers from the lower back of four randomly picked specimens of *T. phasianellus*. B. Lower back feathers of *T. cupido*, of the races *pallidicinctus*, *attwateri*, *pinnatus*, and *cupido*. C, D. Breast feathers of *T. cupido* and *T. phasianellus*, respectively. C. Examples of the races of *T. cupido* in the same order as that for the back feathers in B.

phasianellus and *T. cupido* (including various races and "pallidicinctus") is depicted in figure 3 (note also the variation in *phasianellus* and the approach its pattern shows to that of *cupido*). It is readily apparent that no fundamental difference in pattern is involved. The "peculiarities" in barring of *pallidicinctus* are readily explainable on the basis of a tendency toward broader barring in *T. c. cupido* and *T. c. pinnatus*, and narrower barring in *T. c. attwateri* and *T. c. pallidicinctus*. It is noteworthy that *attwateri* is intermediate in pattern between *pallidicinctus* and the other two races. The narrow, split bars of *pallidicinctus* may have resulted from the effects of selection relating to xeric conditions in the dry plains it inhabits.

The downy young of *T. "pallidicinctus"* has been described by Sutton (1964). Through Dr. Sutton's kindness I was able to borrow his material of that form for comparison with *T. cupido* (races *pinnatus* and *attwateri*). The downy young of *T. "pallidicinctus"* are virtually identical in pattern with those of *T. c. pinnatus*. Although the general tone of color in the young of *pallidicinctus* averages paler than that of the young of *T. c. pinnatus*, paler specimens of the latter exactly match the downy young of *T. "pallidicinctus."* Thus, there are no differences between the natal plumages of these forms to compare with those differences that exist between the downy young of *T. cupido* and *T. phasianellus*. It is noteworthy that two downy young specimens of *T. c. attwateri* are distinguishable from those of *T. c. pinnatus* and *T. "pallidicinctus"* by virtue of their reduced head markings (the markings are smaller in size, and there are but one or two tiny postocular black marks, rather than the one small and two larger markings evident in young of the other two forms). Thus, the natal plumage of *T. c. attwateri* differs more from that of *T. c. pinnatus* than does that of the supposed species *pallidicinctus*.

Jones (1964) cited other differences between the two "species" of prairie chicken. The greater prairie chicken has cervical vocal sacs which are orange lined with red, whereas the lesser prairie chicken has red vocal sacs. The booming notes of the greater prairie chicken are lower pitched (correlated with size?). Habitat differences described by Jones (1963) indicate only that the two forms occupy different habitats; since the prairie chickens studied had no "choice" of the habitat seemingly "preferred" by the other, no difference in habitat "preference" was actually proved. Other differences cited by Jones (1964) are of questionable value in relation to possible isolating mechanisms, since he did not take into account variation within *T. c. pinnatus*, or among *pinnatus*, *cupido*, and, especially, *attwateri*.

Holmes (1963) has studied the leg musculature of *T. cupido*, *T. phasianellus*,

and *T. pallidicinctus*. He found 17 relatively minor differences between *T. cupido* and *T. phasianellus*, but only one trivial difference between the former and *T. pallidicinctus*.

The differences between *T. cupido* and *T. "pallidicinctus"* do not compare in magnitude with those between the hybridizing, closely related species *T. cupido* and *T. phasianellus*. Indeed, in some respects *cupido* and *pallidicinctus* do not differ so much as do intergrading populations within the species *Dendragapus obscurus* and "*Canachites*" *canadensis* (Ridgway and Friedmann, 1946). Since *T. cupido* and *T. pallidicinctus* are allopatric, taxonomic judgment of their status must be based on a comparison of their differences with those observed among other species of grouse, as well as within intraspecific populations of various grouse. Such a comparison indicates that the differences between *cupido* and *pallidicinctus* fall short of those that we would expect to find if these forms were indeed distinct species; hence I consider them conspecific.

Of the two species of prairie grouse, *T. phasianellus* may be less specialized, hence more like the ancestral *Tympanuchus* than *T. cupido*. The sharp-tailed grouse occupies grassland-woodland edge habitat, whereas *T. cupido* is the only essentially grassland grouse. The well-developed vocal sacs and elongate lateral neck feathers of the prairie chicken appear to be specializations involved in its displays; the sharp-tailed grouse has poorly developed vocal sacs and rudimentary (or no) modified lateral neck feathers. Although the evidence is inconclusive, I suspect that *phasianellus* more nearly resembles the ancestral prairie grouse than does *cupido*.

BONASA STEPHENS, 1819, AND TETRASTES KEYSERLING AND BLASIUS, 1840

Bonasa and *Tetrastes* are, respectively, North American and Eurasian genera, respectively containing one and two species. These grouse inhabit coniferous or mixed deciduous-coniferous woodland. *Bonasa* was erected by Stephens (1819) on the basis of its erectile neck feathers; within *Bonasa* he included the ruffed grouse (*B. umbellus*) and the "heath hen" (*Tympanuchus cupido*). *Tetrastes* was described by Keyserling and Blasius (1840) chiefly on the basis of the partly feathered tarsi and 16 rectrices of *T. bonasia*.

These two genera have long been maintained adjacently in taxonomic lists (Ogilvie-Grant, 1893; Peters, 1934). Kleinschmidt (1949, 1952) considered *Tetrastes bonasia*, *T. sewerzowi*, and *Bonasa umbellus* as comprising a "Weltformenkreis" of hazel grouse. These grouse share many features, especially the following: (1) alone among the grouse their tarsi are only partly feathered; (2) their natal plumages are very similar (Kleinschmidt,

1952, p. 34); (3) their adult plumages are similar (barring below, vermiculations above, short crest, neck ruff in *B. umbellus* and tendency toward a ruff in both species of *Tetrastes* [Ogilvie-Grant, 1893, pp. 91, 93]); (4) unlike other grouse they lack inflatable superciliary "combs"; and (5) they show similarities in behavior, including solitary courtship display by the males, and the drumming of male ruffed grouse (Bump *et al.*, 1947) and hazel grouse (Kleinschmidt, 1952). These similarities unite these genera, and separate them from other genera of grouse. *Tetrastes* seems distinguishable from *Bonasa* because of its lack of a ruff, but traces of the ruff are occasionally evident in both species of *Tetrastes*, as noted above. *Bonasa umbellus* usually has 18 rectrices and *Tetrastes* (sp.) 16, but I have above indicated variation of from 14 to 20 rectrices in *B. umbellus*. The few specimens of *Tetrastes* that were examined showed the typical 16 rectrices, but it is likely that some variation occurs in *Tetrastes*, as in other grouse. At any rate this character is not useful for delimiting genera of grouse, so it cannot be so utilized here. I agree with Kleinschmidt (1949, 1952) that these three species of grouse are well-differentiated geographical representatives derived from a common ancestor. Their differences are of the nature one would expect between congeneric species of grouse. Certainly the features of *Bonasa* do not warrant maintaining it as a monotypic genus. I therefore advocate merger of *Tetrastes* into *Bonasa*.

Additional features of *Bonasa*, as defined herein, include a rather long tail with subequal rectrices, and a subterminal band or bands. *Bonasa* exhibits only slight sexual dimorphism. Cervical vocal sacs are absent or vestigial (Wing, 1946). The partly feathered tarsi are short relative to the toes. The color of the eggs is similar to that of eggs of *Dendragapus* and *Lagopus leucurus*, except that the markings are smaller and fewer in number. The downy young are pale yellowish below and strongly chestnut to rufous-colored dorsally. Head markings in the natal plumage are few and are more numerous in *B. sewerzowi* (loral mark, orbital lines, frontal mark traces, trace of black border of chestnut patch) than in other species of *Bonasa*.

The three species of *Bonasa* form a morphological series of *B. sewerzowi*-*B. bonasia*-*B. umbellus*. This is shown by a comparison of several plumage characters in table 4. *Bonasa umbellus* clearly exhibits a more specialized plumage than *B. sewerzowi*, and *B. bonasia* is intermediate. Data for characters other than those given in the table yield similar results. *Bonasa umbellus* has a well-developed ruff that is absent from or rudimentary in *sewerzowi* and *bonasia*. The latter two species, as does *Dendragapus falcipennis*, normally have 16 rectrices, but *B. umbellus* has 18. *Bonasa sewerzowi* is generally barred like *D. falcipennis* and has a less-complicated pattern of ver-

TABLE 4
Color Comparison of Some Adult Grouse

Character	<i>Dendragapus</i> <i>falcipennis</i>	<i>Bonasa</i> <i>seuerzovi</i>	<i>Bonasa</i> <i>bonasia</i>	<i>Bonasa</i> <i>umbellus</i>
Hind neck	Moderately barred	Moderately barred	Finely barred	Faintly barred
Upper back	Broddly barred; white tips and shaft streaks	Broadly barred; no shaft streaks	Narrowly barred or vermiculated; no shaft streaks	Streaks, blotches and bars; white tips and shaft streaks
Central rectrices	Central 2 brown, vermiculated	Central 4 brown, vermiculated, narrowly barred	Central 2 brown, vermiculated, with narrow obscure bars	Central 2 like other rectrices; or as in <i>B. bonasia</i>
Tail	Black; white tip; bases often barred or vermiculated	Black and white barred; white tip	Vermiculated; broad dark subterminal band and whitish tip	Vermiculated with narrow bars; narrow dark subterminal band, with whitish tip
Throat, ♂	Black; obscure border	Black; narrow border	Black; white border	White; sides black at feather tips
Throat, ♀	White with black margins; or barred	Black and white barred	White; sides black at feather tips; or barred	White; sides black at feather tips

miculations, streaks, and blotches than does *B. umbellus*; *B. bonasia* is intermediate. A similar progression holds for natal plumages, except that the trend is from the bolder, complex, *Dendragapus*-like pattern approached by *B. sewerzowi*, to a more uniform pattern with fewer markings exhibited by *B. umbellus*. Although this sequence is not to be construed as a phylogenetic series, *B. sewerzowi* appears more like the ancestral species of *Bonasa* than does either of the other species. *Bonasa* seems related to *Dendragapus*, and probably originated from pre-*Dendragapus* stock. The only known hybrids involving *Bonasa* are between *B. bonasia* and several species of *Lagopus*, a genus that is also closely related to *Dendragapus*.

THE ORIGIN, EVOLUTION, AND CLASSIFICATION OF GROUSE

The grouse comprise a group of closely related genera warranting only subfamilial recognition within the Phasianidae (Mayr and Amadon, 1951; Brodkorb, 1964; Vaurie, 1965). A brief diagnosis of this subfamily is presented in the Appendix. The subfamily appears to have originated somewhat recently from pheasant-like ancestors in North America. I consider the following as evidence for its rather recent origin: (1) the close interrelationships (see above); (2) the close relationship with phasianine pheasants, as indicated by the frequency of hybrids between grouse and pheasants (Gray, 1958, listed hybrids between *Phasianus colchicus* and six "genera" of grouse, including hybrids with three species of *Lagopus*); and (3) the restricted northern Holarctic distribution (grouse fail to reach Mexico in North America, and do not reach the Himalayas in Eurasia).

The distributions of extant species of grouse and the occurrence of fossil grouse are indicated in table 5. Several recent and three fossil genera of grouse are known in the fossil record of North America, dating back to the Miocene, whereas a Pleistocene species of the modern genus *Tetrao* appears to be the only fossil Eurasian grouse (Brodkorb, 1964). Ancestral phasianid stock in North America apparently evolved into New World quail (Odontophorinae), turkeys (Meleagridinae), and grouse (Tetraoninae), thus accounting for the absence of the Phasianinae from this continent. Stegmann (1938) and Mayr (1946) have previously suggested a North American origin for the grouse, and this view is strongly supported by the present and past distribution of grouse as summarized in table 5. The other New World galliform birds, the Cracidae and Opisthocomidae, are much more ancient, and their nearest possible phasianid relatives are to be found in the Old World rather than the New World.

TABLE 5
DISTRIBUTION OF GENERA AND SPECIES OF GROUSE

North America		Eurasia
<i>Lagopus</i>		<i>Lagopus</i>
<i>lagopus</i>		<i>lagopus</i>
<i>mutus</i>		<i>mutus</i>
<i>leucurus</i>		
<i>Bonasa</i>		<i>Bonasa</i>
<i>umbellus</i>		<i>bonasia</i>
		<i>sewerzowi</i>
<i>Dendragapus</i>		<i>Dendragapus</i>
<i>obscurus</i>		<i>falcipennis</i>
<i>canadensis</i>		
		<i>Tetrao</i>
		<i>urogallus</i>
		<i>parvirostris</i>
		<i>tetrix</i>
		<i>mlokosiewiczi</i>
<i>Centrocercus</i>		
<i>urophasianus</i>		
<i>Tympanuchus</i>		
<i>cupido</i>		
<i>phasianellus</i>		
2	Endemic genera	1
5	Genera	4
9	Species	9
<u>3</u>	<u>Fossil genera</u>	0
<u>4</u>	<u>Fossil species</u>	0
<u>2</u>	<u>Modern genera</u>	0
<u>5</u>	<u>Fossil species</u>	1

The relationships of extant species of grouse are depicted in a dendrogram (fig. 4). The line of grouse containing the modern group (*Dendragapus*) most like ancestral grouse is indicated at the center of the diagram. Only extant species are indicated on the diagram, and the degree of divergence is shown within genera, but not between genera. Species of phylogenetically older genera (e.g., *Bonasa*) may have diverged less from the ancestral grouse than those of more recent genera (e.g., *Centrocercus*, *Tetrao*). *Dendragapus* contains species that together encompass a greater number of features of the ancestral grouse than do species of any other extant genus. Other genera (*Bonasa*, *Tetrao*, *Lagopus*, *Tympanuchus*) contain

species that share some features with the ancestral grouse and *Dendragapus*. The species believed to be most like the ancestral form are *D. falcipennis*, *D. canadensis*, and *Bonasa sewerzowi*. Other species that may share some features of the ancestral grouse are *Tetrao mlokosiewiczi*, *T. parvirostris*, *Bonasa bonasia*, *Lagopus lagopus*, *L. mutus*, and *Tympanuchus phasianellus*. The ancestral grouse was probably a woodland-edge species, generally colored like the grouse mentioned above, monogamous in habits, and with no display structures other than inflatable superciliary combs.

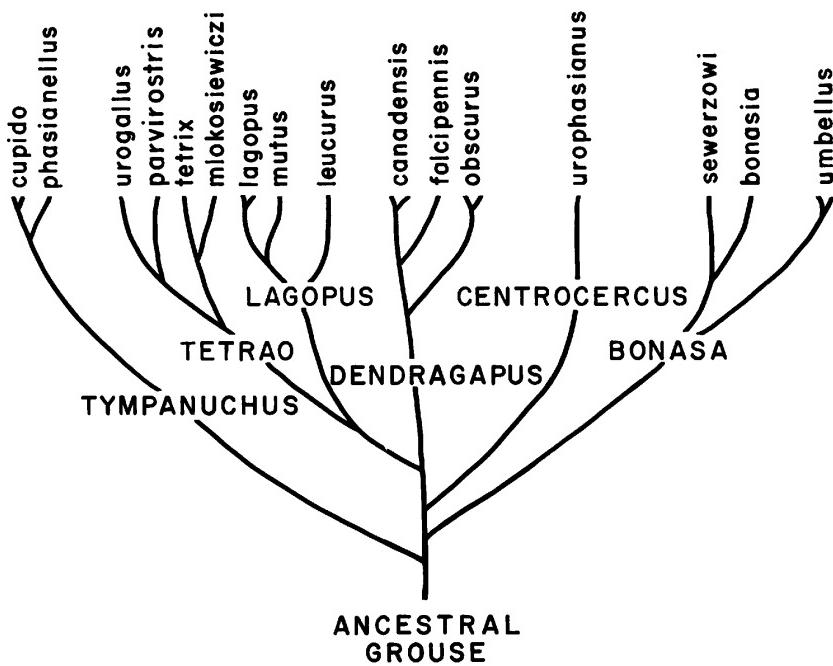


FIG. 4. Dendrogram of grouse relationships. See discussion in text.

The earliest offshoot of the ancestral grouse was probably a grassland-woodland-edge form, the ancestral species of *Tympanuchus*. A Miocene species placed in *Tympanuchus* is the oldest known member of any extant genus (Brodkorb, 1964). At some later time there independently evolved from pre-*Dendragapus* stock the ancestors of *Bonasa*, *Lagopus*, and *Centrocercus* (not necessarily in that order). *Tetrao* probably evolved somewhat later from an early form of *Lagopus* that shared some features of the two genera.

Three genera (*Tympanuchus*, *Centrocercus*, *Lagopus*) contain species in-

habiting essentially open country and woodland edges. The other genera (*Dendragapus*, *Bonasa*, *Tetrao*) are comprised of woodland species, although individual species (e.g., *Tetrao tetrix*) may prefer woodland edges. The evolution of woodland and grassland grouse took place in North America, where possible competitors in the form of open-country pheasants (Phasianinae), bustards (Otididae), and tinamous (Tinamidae) were lacking. Most of the genera evolved in North America, with *Tetrao* the only definite Palearctic derivative and *Bonasa* a possibility for such an origin (although it is equally likely that the latter evolved in North America).

It is always difficult to arrange the genera and species of a family or subfamily in linear sequence. The relationships shown in figure 4 can be expressed in several possible sequences. Recognizing the impossibility of arriving at a sequence that is satisfactory in all respects, I offer the following classification of the grouse:

- { *Dendragapus falcipennis* (Hartlaub), 1855
- { *Dendragapus canadensis* (Linnaeus), 1758
 - Dendragapus obscurus* (Say), 1823
 - Lagopus lagopus* (Linnaeus), 1758
 - Lagopus mutus* (Montin), 1776
 - Lagopus leucurus* (Richardson), 1831
- { *Tetrao mlokosiewiczi* Taczanowski, 1875
- { *Tetrao tetrix* Linnaeus, 1758
 - { *Tetrao parvirostris* Bonaparte, 1856
 - { *Tetrao urogallus* Linnaeus, 1758
 - Bonasa sewerzowi* (Przewalski), 1876
 - Bonasa bonasia* (Linnaeus), 1758
 - Bonasa umbellus* (Linnaeus), 1766
 - Centrocercus urophasianus* (Bonaparte), 1827
 - Tympanuchus phasianellus* (Linnaeus), 1758
 - Tympanuchus cupido* (Linnaeus), 1758

Brackets enclose those species that comprise superspecies. Species within each genus are listed from the one considered least specialized to that considered most specialized. The generic arrangement is less than ideal. *Bonasa*, *Centrocercus*, and *Tympanuchus* are individually related to *Dendragapus*, and their arrangement in this sequence is purely arbitrary. *Dendragapus* is more primitive than the other genera and is listed first. The line of specialization leading from *Lagopus* to *Tetrao*, and the close relationship of *Lagopus* and *Dendragapus*, are indicated by this generic arrangement.

Table 6 offers a comparison of this generic classification with several others. Significant are the differences in arrangement (discussed above) and the difference in number of genera recognized. The number of species per genus is 2.67, with 16 species recognized (or 3.17 if 19 species

TABLE 6
NUMBER AND ARRANGEMENT OF GENERA AND SPECIES AND STATUS OF GROUSE AS A GROUP

	Peters (1934)	American Ornithologists' Union (1957) ^a	Present Paper
Genera and number of species	<i>Tetrao</i> , 2 <i>Lyrurus</i> , 2 <i>Dendragapus</i> , 1 <i>Lagopus</i> , 4 <i>Canachites</i> , 2 <i>Falcipennis</i> , 1 <i>Tetraastes</i> , 2 <i>Bonasa</i> , 1 <i>Pedioecetes</i> , 1 <i>Tympanuchus</i> , 2 <i>Centrocercus</i> , 1	(<i>Tetrao</i> , 2) (<i>Lyrurus</i> , 2) <i>Dendragapus</i> , 1 <i>Canachites</i> , 1 (<i>Falcipennis</i> , 1) (<i>Tetraastes</i> , 2) <i>Bonasa</i> , 1 <i>Lagopus</i> , 3 (4) <i>Pedioecetes</i> , 1 <i>Tympanuchus</i> , 2 <i>Centrocercus</i> , 1	<i>Dendragapus</i> , 3 <i>Lagopus</i> , 3 <i>Tetrao</i> , 4 <i>Bonasa</i> , 3 <i>Centrocercus</i> , 1 <i>Tympanuchus</i> , 2
Number of genera	11	11	6
Number of species	19	?	16
Taxonomic rank	Family Tetraonidae	Family Tetraonidae	Subfamily Tetraoninae

^a Parentheses enclose genera not considered in this publication.

are recognized), compared with 1.73 species per genus for those recognized by Peters (1934). The reduction in number of genera appears biologically and practically reasonable.

SUMMARY

Egg color and size, and the natal plumages of grouse were studied. The various genera and species of grouse were grouped according to these characters, and the groupings are similar for both characters. An examination of the tails of North American grouse clearly indicates that the number of rectrices is too variable to be taxonomically useful at the generic level. One species (*Dendragapus obscurus*) exhibits almost the entire range of variation in rectrix number for all grouse (16–22 rectrices, versus 14–22 for all grouse). In addition to these features, attention was also devoted to the juvenal plumage and definitive adult plumages.

An appraisal of the existing genera of grouse was based on these studies, and also on evaluation of other "generic" characters, and consideration of biological phenomena such as interbreeding, predation selection on woodland versus grassland grouse, and various sympatric interactions. As a result, these five genera do not merit recognition: *Lyrurus* (merged in *Tetrao*), *Canachites* and *Falcipennis* (merged in *Dendragapus*),

Pedioecetes (merged in *Tympanuchus*), and *Tetrastes* (merged in *Bonasa*). The major groups of grouse are the stem *Dendragapus* group, including its offshoot the *Lagopus-Tetrao* subgroup, the prairie grouse group (*Tympanuchus*), the *Bonasa* group, and the *Centrocercus* group. The last three groups appear to have been independently derived from ancestral *Dendragapus* stock. There are recognized 16 species of grouse in six genera, characteristics of which are defined.

Paleontological and zoogeographic evidence indicates a North American origin for grouse. This group comprises at most a subfamily of the Phasianidae, which evolved along with turkeys (Meleagridinae) and New World quail (Odontophorinae) from early North American phasianid stock. A diagnosis of the Tetraoninae is presented.

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APPENDIX: DIAGNOSIS OF THE SUBFAMILY TETRAONINAE

Distribution Holarctic; habitat mainly woodlands, but also tundra and (in the New World) grasslands; adult color patterns generally with

brown's, gray's, black and white in a mixture of bars and streaks, but some have all-white plumages and others exhibit solid gray or black on the head, neck, and under parts; there are many plumage modifications associated with displays, such as pointed and curved rectrices, elongate neck feathers, throat "ruffs," narrowed primaries; precocial young have a natal plumage similar to that of other phasianids; juvenal plumage typically phasianid; complicated molt pattern in some species; tarsi fully (usually) or partly feathered, and toes also feathered in one group (some pheasants, such as *Lerwa* and *Tetraophasis*, have partly feathered tarsi like those of some grouse); tarsometatarsi short, less than half of the length of the tibiotarsus; area around nostrils feathered (true also of the phasianine *Tragopan temmincki*); bill relatively small, with rounded culmen; wings relatively short, rounded; tail variable in form and length, and rectrices variable in number (14 to 22), even within individual species; toes pectinate in most species, especially in winter; erectile red or yellow "comb" over the eyes, better developed in males; inflatable, brightly colored cervical vocal sacs in males of several species; pelvis very shallow and wide (unique among galliform birds; Holman, 1964, p. 248); hypoleideum triangular in shape; postacetabular region very broad; elaborate courtship and territorial displays in many species, especially those exhibiting "lek" behavior; most species polygamous, some monogamous; largely sedentary, except for a few of the more northern species.

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